Grasping Behavior in Tufted Capuchin Monkeys (*Cebus apella*): Grip Types and Manual Laterality for Picking up a Small Food Item

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ABSTRACT   This study investigates prehension in 20 tufted capuchins (*Cebus apella*) in a reaching task requiring individuals to grasp a small food item fixed to a tray. The aim was twofold: 1) to describe capuchins' grasping techniques in detail, focusing on digit movements and on different areas of contact between the grasping fingers; and 2) to assess the relationship between grip types and manual laterality in this species. Capuchins picked up small food items using a wide variety of grips. In particular, 16 precision grip variants and 4 power grip variants were identified. The most frequently used precision grip involved the distal lateral areas of the thumb and the index finger, while the most preferred kind of power grip involved the thumb and the palm, with the thumb being enclosed by the other fingers. Immature capuchins picked up small food items using power grips more often than precision grips, while adult individuals exhibited no significant preference for either grip type. The analysis performed on the time capuchins took to grasp the food and withdraw it from the tray hole revealed that 1) precision grips were as efficient as power grips; 2) for precision grips, the left hand was faster than the right hand; and 3) for power grips, both hands were equally quick. Hand preference analysis, based on the frequency for the use of either hand for grasping actions, revealed no significant hand bias at group level. Likewise, there was no significant relationship between grip type and hand preference. Am J Phys Anthropol 125:30–41, 2004. © 2004 Wiley-Liss, Inc.

The prehensile hand is one of the major traits distinguishing the order of Primates from other mammal species. All primates, in fact, are able to grasp an object and hold it partly or wholly within only one hand (Napier, 1980). Focusing on the prehensile movements of the human hand, Napier (1956) identified two main grip patterns: 1) the *power grip*, in which the object is held between the surface of the partly flexed fingers and the palm, with the thumb acting as reinforcing agent; and 2) the *precision grip*, in which the object is pinched between the tips of the fingers and the opposed thumb. According to Napier (1956, 1980), anatomical features that facilitate the human ability to grasp objects precisely and move them with great dexterity include a fully opposable thumb, broad surface of the finger pads, and relatively long thumb with respect to the index finger, which permits full pad-to-pad contact between them. He argued that only humans are capable of applying efficient precision grips to the objects.

Although, compared to the human hand, the hands of nonhuman primates display significant differences in certain anatomical features relevant to prehensile activity, the relationship between hand morphology and degree of manual dexterity of various species is still unclear. For example, although

great ape thumbs such as those of Old World monkeys (with the exception of the thumbless Colobinae) are fully opposable, they are proportionally shorter than those of all other catarrhine primates. Because of this anatomical constraint, Napier (1980) claimed that great apes cannot apply a functional precision grip. Nevertheless, recent behavioral studies showed that these nonhuman primate species are capable of grasping small objects efficiently, using a variety of precision grasping techniques, although, unlike some Old World monkeys (e.g., baboons and macaques), they did not achieve the pad-to-pad opposition between the first two digits, i.e., the typical contact pattern of humans (Boesch and Boesch, 1993; Butterworth and Itakura, 1998; Christel,

1993, 1994; Christel et al., 1998; Hopkins et al., 2002; Jones-Engel and Bard, 1996).

Another intriguing example regarding the somewhat unclear relationship between hand morphology and manual dexterity in nonhuman primates comes from data on tufted capuchin monkeys (*Cebus apella*), a New World primate species. Compared to Old World primates, New World monkey thumbs are proportionally longer, but have a different kind of carpo-metacarpal joint that imposes constraints on the extent to which they can oppose to other digits. In these species, the typical hinge-shaped joint of the thumb at the base of the palm allows abduction/adduction and flexion/extension movements, but not rotational movement, the key factor in opposability (Napier and Napier, 1967). For a long time it was thus held that no New World monkey species could grasp objects with precision (Bishop, 1964; Napier, 1980; Napier and Napier, 1967). However, comparative behavioral studies showed that capuchin monkeys stand out from other plathyrrine species for their high degree of manual dexterity (Fragaszy, 1986; Lacreuse and Fragaszy, 1997; Panger, 1998), for their frequent use of functional precision grips, which mainly involve the lateral aspects of digits for picking up small objects, and for their capacity to perform relatively independent movements of the digits (Christel and Fragaszy, 2000; Costello and Fragaszy, 1988).

The ability to perform highly fractionated movements of the fingers depends on the number and extension of corticomotoneuronal connections that innervate the hand (Kuypers, 1981; Lemon, 1993; Muir and Lemon, 1983; Shinoda et al., 1981). Data on tufted capuchins show that a dense neuronal substrate of direct corticospinal motoneurons innervates their fingers (Bortoff and Strick, 1993). Moreover, in this species, the distribution of these corticospinal terminations is similar in extension to that observed in humans and chimpanzees. It thus seems that features of the neural substrate controlling capuchin hand movements represent a basic factor for explaining their manual dexterity.

The primary aim of the present study is to describe the different grasping techniques of capuchins, focusing on digit movements during prehension of a small food item and, in particular, on the different contact areas between the grasping fingers, as they have been defined for several catarrhine species (Christel, 1993, 1994; Christel et al., 1998). Although previous studies showed that tufted capuchins are capable of a degree of precision, notwithstanding the morphological differences with catarrhine primate hands, their different grasping variants, as well as the different finger areas coming into contact with the food, have not been examined in detail. Moreover, although it was found that capuchins can also use power grips for picking up small objects, no systematic account of these grasping patterns has been given for this species.

The second aim of the present study is to assess the relationship between different grasping patterns and manual laterality in this species. Most humans show a right-hand/left-hemisphere superiority for a wide range of manipulative behaviors (Annett, 1985; Corballis, 1991; Kimura, 1979). However, there is evidence that human handedness is a multidimensional phenomenon: hand preference and performance can vary as a function of the level of motor skills required to perform tasks. For example, fine sequential finger movements are more likely to produce lateral asymmetries than are simpler actions (Elliott and Chua, 1996; Healey et al., 1986; Marchant et al., 1995; Steenhuis, 1996; Steenhuis and Bryden, 1989). Moreover, the prevalence of right-handedness in adult individuals may reflect the role of culture in shaping behavior, especially during childhood development. For example, in some cultures and religions, the natural use of the left hand is strongly discouraged, and specific pressures may be placed on a child to use the right hand for certain activities (Teng et al., 1976).

Research with nonhuman primates likewise indicates that task complexity may affect the expression of manual laterality in several species (Fagot and Vauclair, 1991; MacNeilage et al., 1987). However, the question of whether nonhuman primate asymmetries are analogous to or homologous with those of humans is still under discussion because of several conflicting results concerning monkeys and apes (Corballis, 1997; Hopkins, 1999; McGrew and Marchant, 1997). Indeed, while it is now clear that tasks involving simple motor patterns do not elicit consistent manual asymmetries in a broad range of primate species (Hopkins, 1993; Larson et al., 1989; Vauclair and Fagot, 1993), a less clear picture emerges from data on more skilled activities. For example, several recent studies involving capuchins indicated a group-level right-hand hand bias for reaching actions requiring a strong postural demand (e.g., bipedal stance) or bimanual coordination, while other coordinated-bimanual tasks involving a sequence of problem-solving actions simply enhanced individual hand preference (Spinozzi et al., 1998; Spinozzi and Truppa, 1999, 2002; Westergaard et al., 1998). Likewise, complex tasks involving the use of an object as a tool produce strong individual hand preferences (Westergaard and Suomi, 1994), while haptic tasks, requiring fine digit movements for searching for or discriminating food, elicit group-level left-hand biases in both performance and preference. On the other hand, haptic tasks which do not involve any manipulative demand for food location do not elicit consistent hand biases in capuchins (Lacreuse and Fragaszy, 1996, 1997, 1999; Parr et al., 1997; Spinozzi and Cacchiarelli, 2000). These latter findings are particularly relevant to the aim of the present study, since they seem to suggest that finely tuned finger movements are more likely to induce hand asymmetries in this New World monkey species. Moreover, in

their description of capuchin grip types, Costello and Fragaszy (1988) and Christel and Fragaszy (2000) found that their monkeys tended more frequently to use their right hand for complex digital coordination. However, it is difficult to generalize these results, given the small number of subjects examined (5–6 subjects). In the present study, we further investigate the relationship between dexterity and lateral asymmetry in both performance and preference in a sample of 20 tufted capuchins while they are picking up a small piece of food.

METHODS

Subjects

The subjects were a captive group of 20 tufted capuchins (*Cebus apella*) ranging in age from 6 months–22 years (Mean = 8.0). Immature subjects (<5 years; age range, 6 months–4 years) comprised 5 females and 3 males, while adult individuals (≥5 years; age range, 6.01–22.01 years) included 6 males and 6 females. The monkeys lived in six social groups, each in an indoor-outdoor cage (indoor, 3.0 m long × 1.7 m wide × 3.0 m deep; outdoor, 2.5 × 1.7 × 3.0 m). They were housed at the Institute of Cognitive Sciences and Technologies, Consiglio Nazionale delle Ricerche (C.N.R., Rome, Italy). Each subject was separated from the group solely for the purpose of testing just before each daily testing session. The animals were provided with monkey chow before and after testing, and water was freely available.

Apparatus and design

Subjects were tested individually in their indoor cage. A transparent Plexiglas panel (60 cm long × 40 cm high) with a central square aperture (6 × 6 cm) was mounted on the front wall of the cage. A piece of peanut (approximate dimensions, 12 mm × 3 mm × 3 mm) was used as a stimulus for prehension. It was placed vertically into the central hole (4 mm in diameter × 4 mm deep) of a plastic tray (10 × 10 × 1.5 cm). The tray was fixed to a shelf (20 × 20 × 2 cm) located outside of the experimental cage, and centered in front of the Plexiglas panel opening. The distance between the opening and the food was about 15 cm. Before each trial started, the tray was baited with a food item during the monkey's absence. The monkey was then allowed to position itself in front of the panel, insert an arm through the panel's square aperture, and reach for the food.

Each monkey performed approximately 50 trials, 25 trials per day for 2 days. All trials were recorded simultaneously with two cameras (JVC digital) set to a shutter speed of 1/1,000. The cameras were arranged to capture the ulnar and the radial aspect of the hand. A trial began when the monkey inserted its arm into the panel's aperture. Filming continued until the subject grasped the food and moved it out of camera range.

Scoring

Two observers scored all videos, noting all grasping actions by choice of hand. Grip types and contact areas at fingers were analyzed by means of slow motion and still-frame replay of each prehensile act. If the two scorers did not agree about different areas of contact between the grasping fingers, they checked each video frame to reach consensus. Hand preference for all subjects and movement times for each grasping act were also scored.

Following the approach introduced by Costello and Fragaszy (1988) and extended by Christel and Fragaszy (2000), the following definitions were used to designate grips: 1) *precision grip* is any grip in which the object is grasped between the phalanges of a) the thumb and the finger(s), or b) adjacent digits, without the use of the palm; and 2) *power grip* is any grip which involves grasping the object between fingers and palm, regardless of the position of the thumb relative to the plane of the palm. A power grip was also coded when the item a) was held between the flexed thumb and the palm, or b) was stuck into the palm alone.

Capuchins' grasping patterns were assessed by means of two measures. The first measure calculated the frequency of different grip types used by the monkeys for food retrieval. The second one evaluated differences in efficiency among different grip types. Efficiency was defined as the time capuchins took to grasp the food (from first contact with any part of the hand), and to withdraw it from the hole in the PVC tray, i.e., the latency to grasp.

The assessment of manual laterality was based on hand preference and performance. Hand preference involved the relative incidence of use of either hand for food retrieval. Performance was evaluated comparing the latency of the left and the right hand to grasp for and withdraw the food.

RESULTS

Prehension

Frequency for precision and power grips. Of the total of 973 grasping responses scored from the videotapes, 464 comprised precision grips, and 509 comprised power grips. For each subject, we calculated a grip index (GI) by subtracting the total number of grasping responses performed using power grips from the total number of grasping responses done with precision grips, divided by the total number of power and precision grips. The resulting values, ranging from −1.0 to +1.0, correspond to the percentage of precision grips varying between 0 (i.e., GI = −1.0, corresponding to 100% power grips) and 100 (i.e., GI = +1.0, corresponding to 0% power grips). We applied a one-sample t-test to the group data to assess whether the mean GI scores per subject differed significantly from a chance distribution with a mean of zero. The analysis failed to find any statistically significant deviation from chance (GI scores, mean = −0.037, t (19) = −0.21, $P > 0.10$),
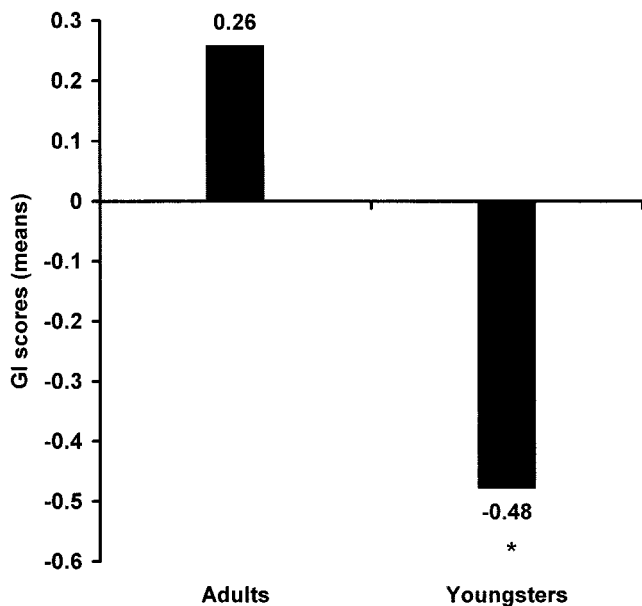
Fig. 1. Grip index (GI) for adult and immature capuchins. *$P < 0.05$.

TABLE 1. Contact areas at fingers during precision grips

Code	Description
1. I dt	At thumb tip.
2. I du	At ulnar aspect of distal phalanx of thumb.
3. I dv	At volar aspect of distal phalanx of thumb (pad).
4. I do	At dorsal aspect of distal phalanx of thumb.
5. I digu	At ulnar aspect of distal joint of thumb.
6. II dt	At tip of index finger.
7. II dr	At radial aspect of distal phalanx of index.
8. II du	At ulnar aspect of distal phalanx of index.
9. II dv	At volar aspect of distal phalanx of index (pad).
10. II digr	At radial aspect of distal joint of index.
11. II digv	At volar aspect of distal joint of index.
12. II mr	At radial aspect of middle phalanx of index.
13. II pigr	At radial aspect of proximal joint of index.
14. II pigv	At volar aspect of proximal joint of index.
15. II pigu	At ulnar aspect of proximal joint of index.
16. III dr	At radial aspect of distal phalanx of middle finger.
17. III dv	At volar aspect of distal phalanx of middle finger (pad).
18. III digv	At volar aspect of distal joint of middle finger.
19. III pigr	At radial aspect of proximal joint of middle finger.

I, thumb; II, index; III, middle finger; d, distal phalanx; m, middle phalanx; p, proximal phalanx; t, tip; r, radial; u, ulnar; o, dorsal; v, volar; ig, interdigital joint.

showing that precision and power grips were used equally often by capuchins as a group.

Independent sample *t*-tests revealed no sex differences in grip types (t (18) = 1.14, $P > 0.10$), but a significant effect due to the subjects' age: mean GI scores of adult subjects (≥5 years) were significantly higher than those of immature individuals (<5 years), (0.26 vs. −0.48; t (18) = 2.33, $P < 0.05$). Thus, the use of a precision grip to seize a small food item was more frequent in adults than in immature capuchins. Moreover, separate one-sample *t*-test analyses for each age class showed that mean GI scores for immature animals, but not for adult individuals, differed significantly from chance (t (7) = −2.49, $P < 0.05$): immature capuchins used more power than precision grips, whereas adult individuals exhibited no significant preference for either grip type (Fig. 1).

Precision grip variants. We distinguished 19 areas of the fingers which came into contact with the peanut during precision gripping. Table 1 gives a description of each contact area and the codes we used to define it.

Capuchins exhibited 16 precision grip variants resulting from the combination of various finger contact areas. We classified them into four more general categories based on anatomic similarity. The first category, *I–II/distal areas*, comprised any observed opposition between the distal phalanges of the thumb and index finger. The second category, *I–II/distal-to-other areas*, comprised any observed opposition between the distal phalanx of the thumb and any part of the middle and proximal phalanges of the index finger. The third category, *I–II, III/distal areas*, comprised any observed opposition between the distal phalanx of the thumb and any part of the distal phalanges of the second and third finger, in combination with each other. The

fourth category, *other variants*, comprised all those precision grip variants that fell outside the above categories. For each category, Table 2 describes each precision grip variant, its occurrence, and the number of subjects exhibiting it.

To assess whether the four precision categories were used differently by capuchins, we performed an analysis of variance (ANOVA) on mean percentages of precision grip responses for each category. The analysis included only those subjects (N = 19) using a precision grip for food retrieval. We found a significant difference across categories (F (3, 54) = 19.1, $P < 0.001$). Post hoc comparison (Tukey honest significant difference (HSD) test) revealed a significantly higher percentage of precision grips involving the distal areas of the first and second digit (*I–II/distal areas*, 61.3%) compared with other precision grip types ($P < 0.001$). Almost all subjects (17 of 19) used it. No difference emerged among the remaining precision grip categories (*I–II/distal-to-other areas*, 13.5%; *I–II, III/distal areas*, 18.0%; *other variants*, 7.2%).

Previous analysis showed that grasping a small food item with the distal phalanges of the thumb and index finger (*I–II/distal areas*) was the most preferred kind of precision grip used by capuchins. A further analysis within this category revealed a significant effect of grip variants (F (6, 96) = 60.3, $P < 0.001$). The mean percentage of the *I du–II dr* variant (75.2%), which involved the ulnar aspect of the distal phalanx of the thumb and the radial aspect of the distal phalanx of the index (Fig. 2a), was significantly higher than that observed for the other six variants. All 17 subjects used it. The remaining *I–II/distal areas* variants were less frequent, and overall were used by no more than 13 of 17 monkeys (*I du–II dv* (N, 7) = 7.2%; *I du–II dt* (N, 2) = 1.1%; *I du–II digr* (N, 6) = 5.2%; *I dt–II dr* (N, 7) =

TABLE 2. Precision grips: ethogram of grip variants by capuchins

Variant	Description	N	Subject
	A) I–II/distal areas		
1. I du–II dr	Ulnar aspect of distal phalanx of thumb, and radial aspect of distal phalanx of index.	237	17
2. I du–II dv	Ulnar aspect of distal phalanx of thumb, and volar aspect of distal phalanx of index.	34	7
3. I du–II dt	Ulnar aspect of distal phalanx of thumb, and index tip.	7	2
4. I du–II digr	Ulnar aspect of distal phalanx of thumb, and radial aspect of distal joint of index.	22	6
5. I dt–II dr	Thumb tip and radial aspect of distal phalanx of index.	21	7
6. I dv–II dr	Volar aspect of distal phalanx of thumb, and radial aspect of distal phalanx of index.	19	5
7. I do–II dv	Dorsal aspect of distal phalanx of thumb, and volar aspect of distal phalanx of index.	9	5
Total		349	17
	B I–II/distal to other areas		
8. I du–II pigv	Ulnar aspect of distal phalanx of thumb, and volar aspect of proximal joint of index.	8	5
9. I du–II pigr	Ulnar aspect of distal phalanx of thumb, and radial aspect of proximal joint of index.	6	2
10. I digu–II pigr	Ulnar aspect of distal joint of thumb, and radial aspect of proximal joint of index.	8	5
Total		22	10
	C) I–II III/distal areas		
11. I du–II d, III d	Ulnar aspect of distal phalanx of thumb, and any part of distal phalanges of index and middle fingers.	57	12
12. I do–II d, III d	Dorsal aspect of distal phalanx of thumb, and any part of distal phalanges of index and middle fingers.	6	5
13. I dv–II d, III d	Volar aspect of distal phalanx of thumb, and any part of distal phalanges of index and middle fingers.	12	6
Total		75	15
	D) Other variants		
14. II du–III dr	Ulnar aspect of distal phalanx of index, and radial aspect of distal phalanx of middle finger.	5	4
15. I dv–III dv	Volar aspect of distal phalanx of thumb, and volar aspect of distal phalanx of middle finger.	5	4
16. I du–II, III	Ulnar aspect of distal phalanx of thumb, and any part of middle or proximal phalanges of index and middle fingers.	8	5
Total		18	9

4.4%; *I dv–II dr* (N, 5) = 3.0%; and *I do–II dv* (N, 5) = 3.9%; see Table 2).

Power grip variants. Table 3 provides a description of the four power grip variants observed in our sample, with their occurrences as well as the number of subjects exhibiting them.

The *enclosed thumb-palm* variant comprised all power grips in which food was grasped and held between the thumb and the palm, with the thumb being enclosed by the other fingers. The *thumb/index-palm* variant was defined as prehension of food between the first two fingers and the palm; during grasping, all fingers were strongly flexed and adducted. In the *thumb-thenar* variant, the food was grasped between the volar aspect of the strongly flexed thumb and the thenar eminence of the palm; all fingers were adducted and strongly flexed. Finally, in the *palm-thenar* grip, the food was grasped between the central area of the palm and the thenar eminence; this kind of grip pattern might be considered a prehension technique, rather than a grip variant, since the palm, but not the fingers, is involved in food retrieval.

The analysis of variance on the mean percentages of grasping responses using the power grips revealed a significant effect of variant type (F (3, 54) = 6.5, P < 0.001). Post hoc analysis revealed that the most used variants, the *enclosed thumb-palm* (44.8 %) and *thumb/index-palm* (42.0%), differed significantly from the *palm-thenar* grip (1.2%). In addition, a significant difference was found between the mean percentages for the *enclosed thumb-palm* and *thumb-thenar* (12.0%) grips.

Efficiency. Statistical analyses to compare efficiency among different grip types were based on the median latency scores for each subject. A dependent *t*-test analysis failed to reveal any significant difference between the latencies for the total precision (294.4 msec) and power grips (396.7 msec), (*t* (17) = 0.93, *P* > 0.10).

In the case of precision grips, we carried out a further analysis to assess whether the latency for the most preferred precision grip types, *I–II/distal areas*, differed from the latency of the other precision grips (collapsed data). The difference was not significant (296.5 vs. 355.3 msec, *t* (16) = −1.49, *P* > 0.10).

A similar analysis, performed for power grip variants, failed to reveal any significant difference between the most frequently used variant, *enclosed thumb-palm*, and the other grip variants (220.0 vs. 300.0 msec, *t* (7) = −1.76, *P* > 0.10).

Finger movements and hand postures in picking up food. In the precision grips, the thumb, slightly flexed, often contacted the object first, pushing it against the index finger. However, in some trials, it was the index finger that touched the food first. After contact, both digits flexed further at the interphalangeal (IP) joints (Fig. 2a). During grasping, the digits did not always move synchronously: the thumb and the index fingers were usually abducted and moved together, while the other fingers were strongly flexed at the metacarpal (MCP) joint and the proximal IP joint. Moreover, in a very small number of cases, we noted that the little finger was
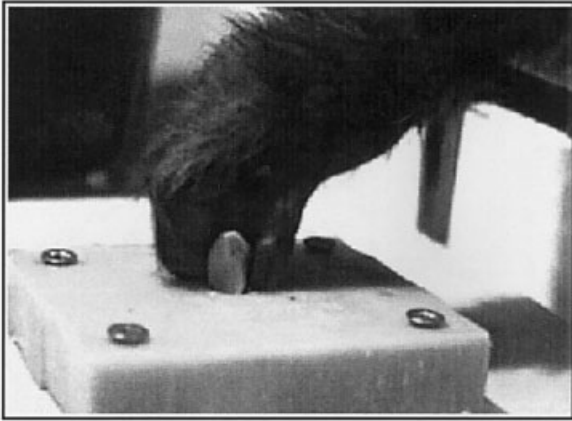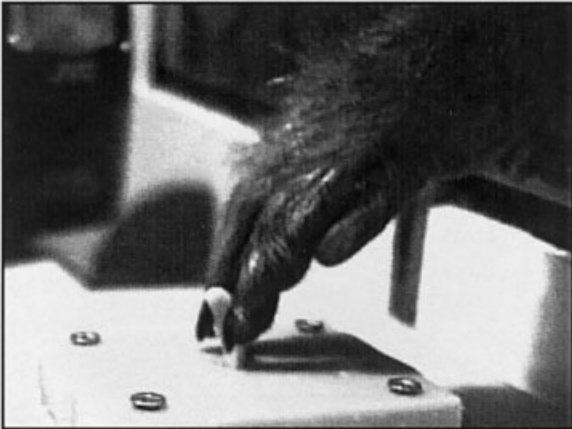
Fig. 2a

Fig. 2b

Fig. 2c

Fig. 2d

Fig. 2e

Fig. 2f

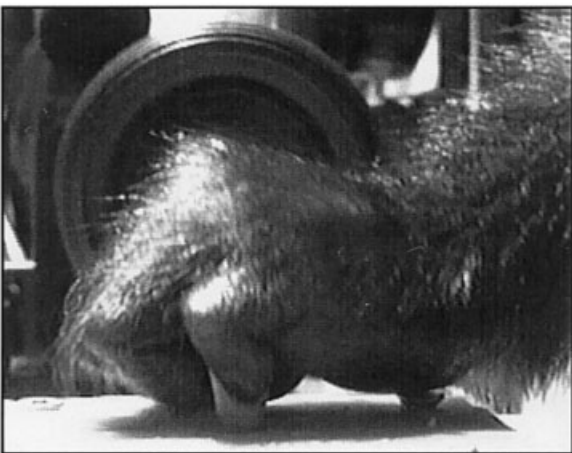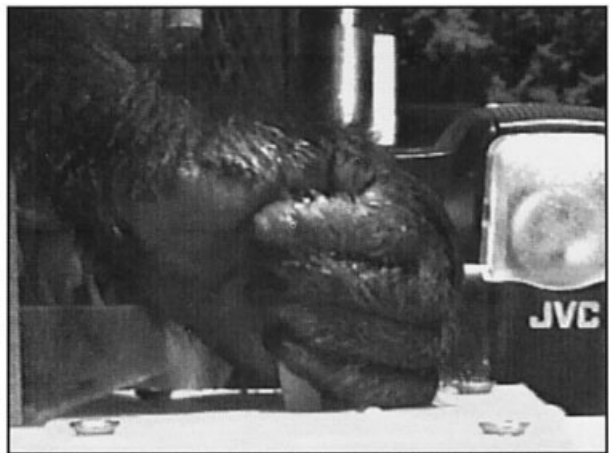**Fig. 2.** a: Precision grip: lateral opposability. **b:** Little finger extended at distal IP joint during precision gripping. **c:** Scissor grip. **d:** Power grip: object makes contact with ulnar aspect of strongly flexed thumb. **e:** Power grip: object grasped between palm and lateral aspects of thumb and index finger. **f:** Power grip: rotational movement of wrist toward radial side of hand.

TABLE 3. Power grips: ethogram of grip variants by capuchins

Variant	Description	N	Subject
1. Enclosed thumb-palm	Object grasped between flexed thumb and palm, with thumb enclosed by other fingers.	274	12
2. Thumb/index-palm	Object grasped between lateral aspects of first two fingers (thumb and index) and palm. All fingers adducted and strongly flexed.	174	17
3. Thumb-thenar	Object grasped between proximal joint of thumb and thenar eminence; thumb and other fingers adducted and strongly flexed.	52	7
4. Palm-thenar	Object held in cavity between central area of palm and thenar eminence; thumb and other fingers adducted and slightly flexed at proximal interphalangeal joint.	9	3
Total		509	19

extended at distal IP joint and slightly flexed at the proximal IP joint, while the third and fourth finger were strongly flexed (Fig. 2b). When capuchins grasped the food in a scissor grip (digits II–III), a pattern occasionally observed in some animals, all fingers were extended or slightly flexed at MCP joints (Fig. 2c).

In power grips, the object typically made contact with the ulnar aspect of the thumb, abducted and strongly flexed at the IP joint (Fig. 2d). After contact, the food was pushed against the radial aspect of the index (Fig. 2e) or against the palmar surface. During grasping, all fingers were adducted and strongly flexed. In the *palm-thenar* grip, all fingers were typically adducted and extended at IP joints and slightly flexed at MCP joints. Convergent movements of the thumb and little finger at the carpal joints allowed the food to be held in the central area of the palm between the thenar pad and the hypothenar eminence.

Once the food had been grasped, the capuchins sometimes rotated the forearm, and therefore the wrist, by about 60–90° around the longitudinal axis, toward its radial aspect, in order to lift the food. The wrist was extended or slightly flexed toward the palmar aspect of the hand. This movement was evident in 59% of all grasping responses, accounting for 72.3% of all power grips (Fig. 2f) and for 44.3% of all precision grips.

Manual laterality

Hand preference. Individual frequencies for the use of the left and the right hand for each grasping action were analyzed using a two-tailed binomial test. Monkeys with z-scores equal to or higher than +1.96 were classified as right-handed, whereas individuals with z-scores equal to or lower than −1.96 were classified as left-handed. Monkeys with z score values lower than +1.96 and higher than −1.96 were classified as ambidextrous. For each subject, a directional handedness index (HI) was calculated using the formula $(R - L)/(R + L)$, in which R and L were the total number of right- and left-handed responses, respectively. The resulting values, ranging from +1.0 to −1.0, situated each monkey's hand preference somewhere on a continuum ranging from strongly right-handed (+1.0) to strongly left-handed (−1.0). The absolute value of the HI (ABS-HI) represents the strength of hand preference, irrespective of its direction.

The individual hand preferences shown by capuchins for all grasping actions are shown as a function of the monkey's sex and age in Table 4. Table 4 also reports the preference data divided into the two main grip patterns (precision and power).

We applied a one-sample *t*-test to the group data to evaluate whether, for all grasping actions, the mean HI scores per subject differed from a chance distribution with a mean of 0. No significant hand bias was evident for the group (mean HI = −0.10; $t(19) = 0.58$, $P > 0.10$). We used independent *t*-tests to evaluate sex or age differences in the direction and strength of hand preference, as determined from HI and ABS-HI scores, respectively. No differences emerged between males and females in either direction (mean HI score, males = −0.42, females = 0.16, $t(18) = -1.7$, $P > 0.10$) or strength in hand preference (mean ABS-HI score, males = 0.78, females = 0.66, $t(18) = -0.84$, $P > 0.10$). Likewise, we found no significant differences between adult and immature capuchins in these measures (mean HI score, adults = −0.22, immature monkeys = 0.08, $t(18) = 0.8$, $P > 0.10$; mean ABS-HI score, adults = 0.75, immature monkeys = 0.66, $t(18) = -0.62$, $P > 0.10$).

To evaluate whether different grip types could elicit significant hand biases in capuchins, the HI scores for precision and power grips were analyzed separately. For each grip type, the analyses included only monkeys performing six or more actions. Therefore, hand preference analyses were restricted to 16 subjects for precision grips and 14 individuals for power grips (see Table 4). No significant hand bias was found for any grip type (precision grip, mean HI = −0.05, $t(15) = 0.24$, $P > 0.10$; power grip, mean HI = −0.10, $t(13) = 0.46$, $P > 0.10$).

A dependent *t*-test was used to assess whether, in individual capuchins, the direction and strength of hand preference for precision grips differed from those shown for power grips. The comparison was restricted to 10 monkeys using either grip six or more times (Table 4). With regard to the direction of lateral bias, we found no significant difference between mean HI scores for precision and power grips (0.02 vs. −0.04, $t(9) = 0.33$, $P > 0.10$). Regarding the strength of hand preference, the mean ABS-HI scores for precision and power grips did not differ (0.67 vs. 0.76, $t(9) = -1.0$, $P > 0.10$).

TABLE 4. Individual hand preferences for precision grips, power grips, and all grasping actions

Subject	Age (years)[1]	Precision grips					Power grips					All grasping actions				
		L	R	HI	z	Preference	L	R	HI	z	Preference	L	R	HI	z	Preference
Females																
Pippi	18.08	25	1	−0.92	−4.6	L***	15	0	−1.0	−3.6	L***	40	1	−0.95	−5.9	L***
Carlotta	16.02	5	20	0.60	2.8	R**	20	0	−1.0	−4.3	L***	25	20	−0.11	−0.6	n.p.
Rame	13.00	0	46	1.0	6.6	R***	3	1				3	47	0.88	6.1	R***
Paprika	10.09	0	0				14	33	0.40	2.6	R**	14	33	0.40	2.6	R**
Paquita	9.08	13	0	−1.0	−3.3	L***	28	7	−0.60	−3.3	L***	41	7	−0.71	−4.7	L***
Panna	6.01	0	8	1.0	2.5	R*	2	39	0.90	5.6	R***	2	47	0.92	6.3	R***
Pacchia	4.00	16	9	−0.28	−1.2	n.p.	3	21	0.75	3.5	R***	19	30	0.22	1.4	n.p.
Pacaja	2.08	0	2				10	40	0.60	4.1	R***	10	42	0.62	4.3	R***
Robiola	1.10	1	0				49	0	−1.0	−6.9	L***	50	0	−1.0	−7.0	L***
Penelope	1.01	4	30	0.76	4.3	R***	4	10	0.43	1.34	n.p.	8	40	0.67	4.4	R***
Virginia	0.06	3	24	0.78	3.8	R***	2	24	0.85	4.1	R***	5	48	0.81	5.8	R***
Males																
Cammello	22.00	6	0	−1.0	−2.1	L*	31	0	−1.0	−5.4	L***	37	0	−1.0	−6.0	L***
Cognac	12.09	41	0	−1.0	−6.3	L***	3	0				44	0	−1.0	−6.5	L***
Gal	10.00	27	23	−0.08	−0.4	n.p.	0	0				27	23	−0.08	−0.4	n.p.
Patè	8.11	51	0	−1.0	−7.0	L***	1	0				52	0	−1.0	−7.1	L***
Narciso	9.06	0	48	1.0	6.7	R***	0	3				0	51	1.0	6.9	R***
Corto	7.09	45	0	−1.0	−6.5	L***	1	0				46	0	−1.0	−6.6	L***
Robin Hood	3.01	3	3	0.0	0.0	n.p.	30	12	−0.43	−2.6	L**	33	15	−0.38	−2.4	L*
Congo	2.04	2	4	0.33	0.4	n.p.	7	36	0.67	4.3	R***	9	40	0.63	4.3	R***
Sandokan	0.06	4	0				59	1	−0.97	−7.4	L***	63	1	−0.97	−7.6	L***

[1] Capuchins under 5 years were considered immature individuals; z, zeta scores; L, left hand; R, right hand; n.p., no preference; HI, handedness index.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

Performance. To assess differences in performance between hands, the latency analysis, based on individual median scores, included only those monkeys using both the left and right hand for each prehensile act (i.e., at least one action with either hand). Hand efficiency was evaluated 1) for all grasping actions, and 2) for grip types.

A dependent *t*-test was used to evaluate whether, for all grasping actions, the latency for the right hand differed from the latency for the left hand. No significant intermanual differences were found: both hands performed equally well in grasping for and withdrawing food (N of subjects = 14, LH = 412 msec, RH = 377 msec, *t* (13) = 0.30, *P* > 0.10). A similar analysis was used to evaluate whether, in individual capuchins, performance was higher with the preferred than with the nonpreferred hand. As shown in Figure 3, latency was lower with the preferred (280 msec) than with the nonpreferred (509 msec) hand (*t* (13) = −2.35, *P* < 0.05). Thus, the hand more often used during the task also allowed the fastest food retrieval.

A different picture emerged when the performance difference between hands was analyzed separately by grip type. For those capuchins using precision grips with either hand (N = 8; see Table 4), the left hand was significantly faster than the right hand (LH = 230 msec, RH = 415 msec, *t* (7) = −2.54, *P* < 0.05). In contrast, for those monkeys using power grips with either hand (N = 11; see Table 4), there were no significant differences in efficiency between the hands (LH = 512 msec, RH = 328 msec, *t* (10) = 1.37, *P* > 0.10; see Fig. 3).
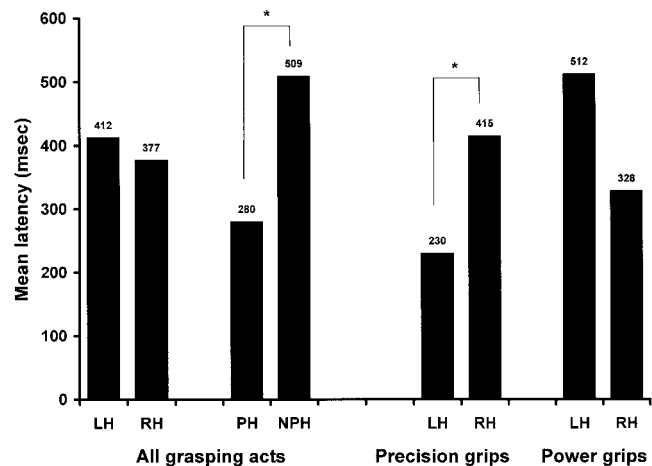

Fig. 3. Performance: hand latency for all grasping acts, and grip type (precision and power). LH, left hand; RH, right hand; PH, preferred hand; NPH, nonpreferred hand. *P < 0.05.

DISCUSSION
Prehension

The results of the present study show that capuchins use a wide variety of grasping patterns, which include different forms of precision and power grips. The small food item we used to assess monkeys' prehensile abilities did not always elicit dexterous prehension: precision and power grips were used with same frequency, and were equally efficient for picking up and holding the object securely.

Immature capuchins were less likely to use precision grips than were adult animals. However, there was high variability in our sample regarding the use

of a particular grip, with the 1-year-old subject showing a very high rate of precise grasping (70.8%), and one of the two 6-month-old capuchins exhibiting the same proportion (51%) of these prehensile forms as the oldest immature individual (i.e., a 4-year-old). Therefore, the ability to apply fine prehensile movements in food retrieval is well-developed in immature individuals, suggesting that their hands already possess some of the structural and functional features related to precision grips.

Napier (1956, 1980) proposed that the index of opposability of the thumb, i.e., the relative length of digit I and digit II, is one of the main anatomical features relevant for precisely grasping objects. Hand morphometry data indicate that, compared with all catarrhine primates, adult capuchins have a higher thumb-forefinger index (Fragaszy et al., 1989). However, in 6-month-old capuchins, the value of this index is slightly lower than in adult individuals (60 vs. 72; Fragaszy et al., 1989). At this age, infants already display all the major elements of the adult manipulative repertoire (Adams-Curtis et al., 2000). Overall these data indicate that the difference between adult and immature animals in exercising precision grips is not linked to maturational factors, but rather to an idiosyncratic tendency of each individual to use a particular grip pattern.

Capuchins exhibited a wide variety of precision grips, involving different areas of contact between the grasping fingers. Most of these grips involved the thumb and forefinger, with the grasping areas being concentrated at the lateral surfaces of the distal phalanges, so that the object made contact with the ulnar aspect of the thumb and the radial aspect of the forefinger. Less often, the monkeys applied precision grips with the object held between the thumb and more than one other finger, or between the lateral aspects of the index and middle finger. Although used infrequently by our monkeys, these gripping forms were applied as rapidly as the more preferred grip variants.

Capuchins were not able to achieve pad-to-pad contact between the thumb and index finger, as humans and, to some extent, some catarrhine species do (Christel, 1993; Christel et al., 1998; Napier, 1980), because of the limited ability of the capuchin thumb to rotate toward the other digits (Napier and Napier, 1967). The lack of pad-to-pad grips as well as the strong preference for lateral thumb-to-index grips in our capuchin sample, a pattern defined recently by Christel and Fragaszy (2000) as "lateral opposability," confirms previous findings for just one species (Christel and Fragaszy, 2000; Costello and Fragaszy, 1988). Christel and Fragaszy (2000) noted that their five tufted capuchins achieved a precision grip by placing the dorsal aspect of the thumb tip against the volar aspect of the index tip, so that objects made contact with the ulnar surface of the thumbnail. In the present study, most of the precision grips observed in our monkeys mainly involved the opposition of the ulnar surface of the distal pha-

lanx of the thumb and the radial aspect of the distal phalanx of the index finger. It is possible that the discrepancies in the findings are due to differences in food location during the tasks. For example, in our study, the food item was placed vertically on a flat board. By contrast, in Christel and Fragaszy (2000), currants and grapes were placed on flat surfaces and also in shallow wells or angled grooves, which required the use of the extreme tips of digits. Nevertheless, as in previous studies, our capuchins exhibited some degree of finger differentiation when grasping food precisely.

The ability to perform highly fractionated finger movements depends on a monosynaptic connection between the primary motor cortex and hand motoneurons (Kuypers, 1981; Muir and Lemon, 1983; Shinoda et al., 1981). Unlike other New World species, capuchins have abundant corticospinal terminations in the cervical spinal cord. As Bortoff and Strick (1993) showed, capuchin monkeys have dense terminations in the ventral horn, particularly in cervical segments where the motoneurons that innervate hand muscles are located.

Besides performing precision grips, the capuchins frequently recovered the food with palmar grips. In most cases, they moved the object with the thumb, pressing it against the palm, while all other digits flexed synchronously around the thumb in a firm grasp. Often they closed the food into the palm, moving all fingers simultaneously, with the thumb flexed in parallel with the other digits. Less frequently, they recovered the small peanut by enclosing it between the strongly flexed thumb and the palm, or between the thenar and hypothenar pads of the palm. This latter technique seemed to involve the coordination of several muscle groups of the carpometacarpal region of the hand that together allowed the hand to be cupped and accommodated to fit the shape of the object.

Westergaard and Suomi (1997) examined capuchin grips for the use of throwing, nut-cracking, and cutting tools. When force was required, the animals often applied two types of power grips, similar to those reported by Marzke and Wullstein (1996) in chimpanzees: the jaw-chuck grip, in which a stone was held tightly against the palm by flexed fingers, with the thumb supporting the object from the side; and the palm-push grip, in which the tool was pushed by the open palm. The present study further adds to the findings made previously, that capuchins are able to apply four other different forms of power grip, even when a small piece of food has to be recovered and no control is needed in order to use an object as a tool.

Once the food has been contacted, a rotation of the forearm, and thus of the wrist, toward the radial side of the hand is observed more often in association with power than with precision grips. This movement, which seems to indicate some degree of flexibility in the wrist joints (Fragaszy et al., 1989), appeared to improve the monkeys' capability for re-

trieving the reward more securely. It is possible that, given the small size of the peanut and the limited ability of capuchins to rotate their thumb in opposition to the other fingers, this rotational movement might facilitate the monkeys' grips, improving the adherence of the food using the palmar surface of their hand.

Manual laterality

It was suggested that manual asymmetry in nonhuman primates can vary with sensorimotor demands of the task as well as with subject sex and age (Fagot and Vauclair, 1991; MacNeilage et al., 1987; Marchant and McGrew, 1991; Ward, 1991). With respect to the former factor, several researchers found that reaching tasks involving finely tuned movements of digits are more likely to induce group-level hand bias than those involving simpler motor patterns (Fagot et al., 1991; King and Landau, 1993; Lacreuse and Fragaszy, 1997, 1999; Spinozzi and Cacchiarelli, 2000; Spinozzi and Truppa, 1999). In the present study, examination of capuchins' hand preference data for all grasping actions, regardless of the type of grip employed by capuchins for food retrieval, failed to reveal any significant lateral bias for the group: most immature and adult individuals of both sexes exhibited consistent hand preferences, but no significant manual asymmetry emerged for the sample. Likewise, when the data were analyzed as a function of the complexity of motor patterns involved in food grasping, no significant preference for the use of either hand was found. Overall, these findings are comparable to those of Christel and Frgaszy (2000) for just one species, and of Jones-Engel and Bard (1996) and Marchant and McGrew (1996) for chimpanzees. As in our study, in those studies no clear pattern in the direction of hand preference emerged among subjects in retrieval of small food items.

In their evolutionary model for handedness in primates, MacNeilage et al. (1987) proposed that a left-hand preference for visually guided reaching and a right-hand preference for fine manipulations evolved in monkeys and apes. Our results for hand preference in capuchins do not support the point of view of MacNeilage et al. (1987), since the preferential use of one hand for fine manipulation (precise grips) was found at the individual but not at population level.

Conversely, examination of performance time data revealed a different pattern of manual asymmetries. Although the peanut retrieval performance of capuchins was not related to left- or right-hand use, it was linked to the preference for one hand. The latency was lower with the preferred than with the nonpreferred hand, indicating that the hand more often used during the task was also the quickest for food retrieval. Overall these findings confirm those previously reported for several nonhuman primates species, such as tamarins (King, 1995), squirrel monkeys (King and Landau, 1993), capuchins (Fra-

gaszy and Mitchell, 1990), macaques (Fragaszy and Adam-Curtis, 1993), and great apes (Christel, 1994), in which latency of grasping or errors in making unimanual retrieval of food were used as measures of hand asymmetry.

On the other hand, a different picture emerges when performance data are examined as a function of grip types used by capuchins for grasping food. The monkeys did not exhibit any performance difference between hands when using power grips, but they showed significant asymmetries for precision grips, with the left hand acting more quickly than the right in picking up the object. Our finding thus supports the prediction that tasks involving finely controlled digit movements elicit consistent group-level manual asymmetry in nonhuman primates. Rigamonti et al. (1998) found a left-hand superiority (in terms of speed of performance) in pig-tailed macaques when using precision grips to remove small food rewards embedded in a vertical array. Christel et al. (1998) examined precise grasping behavior and intermanual differences in performance in three bonobos when grasping small objects. In analyzing the organization of reach-to-grasp movements, they found that bonobos tended to grasp small objects more quickly with the left than with the right hand. Similarly, Jones-Engel and Bard (1996) found that young chimpanzees were more efficient with the left than with the right hand when using fine grip patterns for picking up small objects; conversely, when using power grips, these animals showed they were faster with the right hand than with the left hand. This laterality effect, however, was found only with medium-sized objects. Nevertheless, Hopkins et al. (2002) found a different pattern of results with a large sample of chimpanzees. Using the error rates in grasping small food items as a measure of performance differences between hands, these authors found a significantly higher accuracy for the right hand than for the left hand. Moreover, the error rates for thumb-index responses were lower than middle-index responses or single-digit responses. It should be noted, however, that in Hopkins et al. (2002), in order to evaluate relative prehension skills (their experiment 3), subjects were encouraged to make the same number of grasping responses with each hand, a procedure that allows a better assessment of performance differences between hands.

Finger muscle groups for fine-scale movements in primates are predominantly controlled by the contralateral hemisphere (Brinkman and Kuypers, 1973; Kuypers, 1981, 1985), and some authors suggested that, in humans, the right-hand/left-hemisphere system is more efficient in specifying the precise muscular forces involved in fine finger adjustments (Elliott and Chua, 1996). Given that capuchins, like chimpanzees, macaques, and humans, have a high number of corticomotoneuronal connections innervating their fingers, the left-hand advantage observed for fine grasping movements seems to

reflect a greater right-hemisphere involvement for this prehensile activity. However, this conclusion must be viewed as tentative, since performance analysis was confined to a small subgroup of capuchins. Furthermore, performance differences between hands could not be assessed for highly lateralized individuals, as they almost exclusively used their preferred hand in all trials. Further investigations using experimental procedures imposing the alternating use of hands for grasping food (see Hopkins et al., 2002) could be more helpful in revealing performance differences between hands in nonhuman primates.

CONCLUSIONS

1. Capuchins display a wide variety of prehensile abilities that confirm their capacity, atypical among New World monkey species, to use their hands dexterously during extractive foraging and object manipulation (Fragaszy and Adam-Curtis, 1991; Fragaszy and Boinski, 1995; Panger, 1998). Although they do not possess a true opposable thumb, typical of catarrhine primates, this New World monkey species is able to achieve easily a precision grip by "lateral opposability" (Christel and Fragaszy, 2000), in which the object makes contact with the lateral surfaces of the distal phalanges of the thumb and forefinger. When doing so, they display a certain degree of independent control of fingers.
2. Besides the use of a wide variety of precision grips, capuchins frequently apply different forms of power grips to grasp and withdraw food from the hole in the apparatus. Most of these prehensile grips are associated with a rotational movement of wrist and forearm that probably improves the monkey's ability to retrieve the object firmly with the palm.
3. A consistent performance difference between hands emerged only when grasping actions involved fine digit control for food retrieval: for precision, but not for power grips, the left hand was faster than the right hand. This intermanual difference may suggest a higher involvement of the right hemisphere for this prehensile activity.

ACKNOWLEDGMENTS

We thank two anonymous reviewers and Marianne I. Christel for helpful comments. Thanks are also due to Bioparco S.p.A. for hosting the laboratory where the experiment was carried out.

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